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ARTICLE II.

ON THE HOMOLOGIES OF THE POSTERIOR CRANIAL ARCHES IN THE REPTILIA.

BY E. D. COPE.

Read before the American Philosophical Society, February 5, 1892.

At the meeting of the American Association for the Advancement of Science, held in Troy, N. Y., in 1870, I presented the result of my studies of the arches which distinguish the posterior part of the cranium in the Vertebrata, and especially in the Reptilia. Three arches were considered, which were named, commencing with the inferior in position: the quadratojugal, the zygomatic and the parietoquadrate. Of these the only arch recognized as occurring in the Mammalia was the zygomatic.* In the determination of this arch I followed Cuvier,† and for the following reason. It was supposed that the quadrate bone represented one of the ossicula auditus. As this element in the Mammalia is intracranial, and does not give support to an arch, the zygomatic arch of that class could not be homologous with the arch which it (the quadrate) supports in the Reptilia (the quadratojugal). The zygomatic arch of the latter class would be, on the contrary, that one which originates at the proximal extremity of the quadrate, which would remain on the supposed withdrawal of the latter within the skull as one of ossicula auditus.

Prof. Peters has, however, shown that the quadrate bone is probably not one of the ossicula auditus, and he is followed by Dollo, Albrecht and others. In a study of the osteology of the Permian reptile, *Diopseus leptocephalus* Cope,‡ I came to the conclusion that the quadratojugal arch of that reptile is the zygomatic arch of the

* Proceedings Amer. Assoc. Adv. Sci., XIX, 1870, p. 197.

† Ossements Fossiles, X, Ed. 1836, 14.

‡ *Clepsydraps leptocephalus* Cope. Proceeds. Amer. Philos. Soc., 1884, pp. 30-42. *Diopseus*, gen. nov., described on a later page.

Mammalia, thus coinciding with the opinion as to the homologies of that arch held by Hallmann, Owen and Peters, and as described by Günther in Sphenodon. On further study of the Permian reptiles contained in my collection, and comparison of them with recent orders, I am more than ever convinced of the correctness of this view, and I propose in the present paper to show the evidence on which it rests. It follows, moreover, that if this interpretation be correct, the bone ordinarily called quadratojugal must be called the squamosal or zygomatic, while the bone to which that name is ordinarily applied must receive another name. The element immediately above the true squamosal, which roofs the temporal fossa in the Stegocephali and Cotylosauria, is the supratemporal of Owen,* first described by him among reptiles in Ichthyosaurus. The element immediately above the supratemporal in the Stegocephali, Cotylosauria and Ichthyopterygia is the mastoid of Cuvier and Owen. As it is probably not homologous with the part of the Mammalian skull called by that name, some other one must be found for it. The numerous names given to bones in this region of the skull all apply to the squamosal or supratemporal, so I propose to name this one the *supramastoid*.

Posterior to the supramastoid in the Stegocephalian and in some of the Cotylosaurian skulls, is an element which frequently projects in an angle in the posterior outline, and which corresponds with the element present in the fishes, which Cuvier termed the intercalare. The relation of this piece to the paroccipital of certain reptiles remains to be ascertained.

It is evident that the correct classification and phylogeny of the Reptilia will not be completed without the determination of the homologies of these segments, and the homologies of the arches to which they contribute. In the endeavor to accomplish this analysis I have been much aided by a suggestion made by Dr. George Baur, which has been fertile of valuable results. In a recent paper† he says: "In the oldest Batrachia, the Stegocephalia, we find a continuous dermal covering of the upper and lateral parts of the skull; * * * the number of these dermal ossifications is nearly constant. * * * The complete covering of the skull is for the first time interrupted in the Ichthyosauria and Aëtosauria‡ by the appearance of a supratemporal fossa, which develops between the parietal, squamosal and the upper posterior border of the orbit. The bony arch below the supratemporal fossa, which connects the orbit with the quadrate, is now affected in two different ways: I. The

* Suprasquamosal of Owen is the same; see Palæontology, pp. 168, 174, 198. Seeley uses the term supratympanic for the same.

† American Journal of Morphology, 1889, p. 471.

‡ Or Pseudosuchia.

broad single arch remains single, but becomes more and more slender and can be interrupted. Plesiosauria, Theromora, Mammalia, Squamata (Lacertilia, Pythonomorpha, Ophidia). II. In the broad single arch appears another opening, the infratemporal fossa, forming an upper and lower arch which connects the orbit with the quadrate; Rhynchocephalia; the whole Archosaurian branch (Crocodilia, Dinosauria, Pterosauria); birds." Dr. Baur then proceeds to identify the postorbital arch of the Lacertilia with the quadratojugal or zygomatic arch, expressing the belief that the ancestors of that order never possessed any other quadratojugal arch, and that the present elevated position of the arch in the Lacertilia is due to reduction at the inferior border. Thus the supratemporal of the lizards (squamosal Auct.) would be the equivalent of the quadratojugal of Sphenodon.

In the endeavor to reach a definite conclusion regarding these questions, I have examined my specimens of the Reptilia of the Permian formation, as being most likely to furnish essential facts. I now give the results of this examination.

I. THE REPTILIA OF THE PERMIAN.

I have well-preserved crania which display sutures of the following species: *Chilonyx rapidens* Cope; *Pantylus cordatus* Cope; *Pariotichus megalops* Cope; *Edaphosaurus pogonias* Cope; *Clepsydrops natalis* Cope; *Naosaurus claviger* Cope; *Diopseus leptocephalus* Cope.

The genera *Chilonyx*, *Pantylus* and *Pariotichus* have the temporal fossæ entirely roofed over, thus belonging to the Cotylosauria,* to which must be probably referred the genus *Pariosaurus* Owen, of the South African Karoo formation, and the *Phanerosaurus* of the German Permian. The other genera, excepting *Diopseus*, belong to the Pelycosauria, which is probably the same as the Theriodonta of Owen.

CHILONYX† agrees with the Stegocephalia, and with other Diadectidæ in possessing a distinct *os intercalare*. The component elements of the cranial roof are equal in number and similar in position to those of the Stegocephalian skull, except that the supramastoid extends between the parietal and intercalare to the posterior border of the cranial table (Fig. 2, *Sm.*); and the supraoccipital does not extend onto the superior face of the skull, except as a narrow border. The quadrate bone is directed forwards instead of posteriorly, which causes an anteroposterior abbreviation of the supratemporal and squamosal elements. The elements of the temporal roof

* Cope. American Naturalist, 1880, p. 304; October, 1889. Pariosauria Seeley. Philos. Transac., London, 1889, p. 292.

† Cope, Proceed. Amer. Philos. Soc., 1883, p. 631.

are not exclusively tegumentary, but are identical in character with the bones of the brain case, and the sutures are visible on the under as well as the upper side.

PANTYLUS* agrees with Chilonyx in the composition of its cranial roof with the exception that the suspensorium is vertical and is not directed forwards. The position of the supraoccipital and intercalare cannot be ascertained, owing to the condition of the specimens (Fig. 4, Plate I).

PARIOTICHUS Cope† agrees in the main with Chilonyx, but the supraoccipital is divided medially and is reflected onto the superior face of the skull as in Stegocephali. The intercalare is reduced to a small element, of which a small part appears on the superior face of the skull immediately behind the exterior part of the supramastoid (Fig. 3, Plate I).

It is then these three genera which, according to Baur's theory, represent the type from which the reptiles with posterior cranial bars have been derived by the development of foramina in the temporal roof. Let us see how this has been accomplished in the different types. I commence with the Permian genera.

The Theriodont genus, from the Permian of which I possess the best preserved cranium, is NAOSAURUS Cope (Fig. 7). It is, unfortunately for our purpose, the most extremely modified. The orbit is in the posterior part of the skull, and the muzzle is greatly elevated and compressed. The zygomatic (quadratojugal) is greatly decurved posteriorly, and the supratemporal is accordingly decurved also. The postfrontal (Fig. 7a) is a narrow bone, wider than long, and it has connection with the frontal, parietal and postorbital only. The postorbital is an L-shaped structure, of which the shorter limb is inferior, extending to the jugal, while the longer limb is posterior, extending to the supratemporal, in contact with the parietal. It encloses no foramen with the latter; but it encloses a larger foramen with the jugal, zygomatic and supratemporal at the other boundaries. This is the infratemporal foramen of Baur. Posterior to the parietal is a small transverse element, which appears to be merely adherent to the former. Its determination is not easy at present. The supratemporal is elongate vertically, and narrow anteroposteriorly. Beneath and towards the middle line of the skull is a part of another bone, which may be the paroccipital, or even exoccipital. The pineal foramen is distinct. No parietoquadrate arch.

In CLEPSYDROPS‡ the structure is apparently the same, although the form is much less modified. The quadrate articulation is nearly in line with the maxillary dental series (Fig. 6, Plate II), and the jugal is nearly horizontal; its inferior border

* Cope, *Bullet. U. S. Geol. Survey Terrs.*, 1881 (8vo).

† *Proceeds. Amer. Philos. Soc.*, 1878, p. 508.

‡ Cope, *loc. cit.*, 1878, p. 509.

being concave upwards. No bar extends posteriorly from the postorbital, which joins the supratemporal, enclosing with it the infratemporal foramen. No indication of the supratemporal foramen can be found in the rather mutilated specimen. I think it was not present.

In *EDAPHOSAURUS* Cope (Fig. 5, Plate II), the skull is of a more depressed type than in the preceding genera. The postorbital is mainly preserved, and it is in contact with the frontal (postfrontal) proximally, and sends out no bar posteriorly. There was apparently no supratemporal foramen, but a very large infratemporal, which extended well upwards. There is no parietoquadrate arch. An element, perhaps supraoccipital, terminates in a free appressed apex on each side of the median posterior region. This may be homologous with the small free bone described in *Naosaurus*, in nearly the same position. The stapes is very large, and is at least partially perforated near the expanded proximal extremity. It is probably fully perforated, as I have described it in the *Diopelus leptcephalus* Cope.

In *DIOPEUS* Cope, the supratemporal is elongate in the vertical direction, and as elsewhere, it overlaps the quadrate at the distal extremity. Anteriorly, it sends forwards a process probably for union with the postorbital bone, which is, however, entirely free from the parietal, and encloses a foramen with it, precisely as in *Sphenodon*. It further resembles the corresponding element in *Sphenodon* in sending upwards a branch for union with the parietal. Thus there are in this genus two posterior bars and two foramina, thus differing widely from the other Permian genera of this or any other country known to me. Whether it has a free parietoquadrate arch I do not know, but it is probable that the genus should be referred to the *Rhynchocephalia*, in the neighborhood of *Palæohatteria* Cred. It differs from *Sphenodon* and resembles closely the *Theriodonta* in the absence of an obturator foramen, and in the character of its dentition.* The zygomatic bone is not excavated below, but has a straight outline to its junction with the jugal. The quadrate condyle is double like that of *Sphenodon* and the *Clepsydropidæ* (Fig. 8, Plate II).

The *THERIODONTA* described by Owen appear to have the single cranial arch constructed in the same way as I described above as characteristic of the American forms. I gather this from Owen's figures of the genera *Kistecephalus* Ow., *Galesaurus* Ow., *Scaloposaurus* Ow., *Anthodon* Ow., and apparently *Lycosaurus* Owen.

The *ANOMODONTA* appear to have a differently constructed posterior cranial region. In my study of the skull of *Lystrosaurus* Cope† (*Proceeds. Amer. Ass. Adv. Sci.*, 1870, XIX, p. 205), I showed that this genus possesses an extensive supra-

* *Proceeds. Amer. Philos. Soc.*, 1884, p. 33.

† *Ptychognathus* Owen (preoccupied) ; *Ptychosiagon* Lydekker, 1889.

temporal foramen, and that the bone which bounds it externally consists posteriorly of the supratemporal bone, and not the zygomatic. Anteriorly this bone joins the postorbital, postfrontal and malar. In the Transactions of the Royal Society for 1889, p. 244, Prof. H. G. Seeley analyzes the structure of the skull of *Dicynodon*, which he shows to resemble closely that of *Lystrosaurus*, and his analysis of the posterior arch and foramen is the same as my own in the latter genus. It is evident then that the Anomodonts differ from the Theriodonts in the absence of a zygomatic arch, and in the presence of a supratemporal arch, which is separated from the parietal bone by a supratemporal foramen (Figs. 1-2).

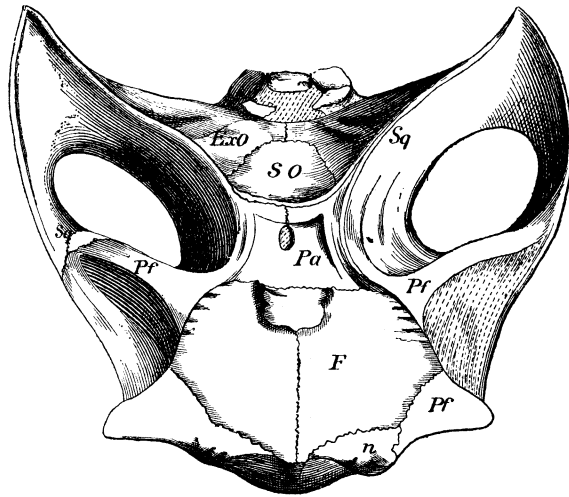


FIG. 1.

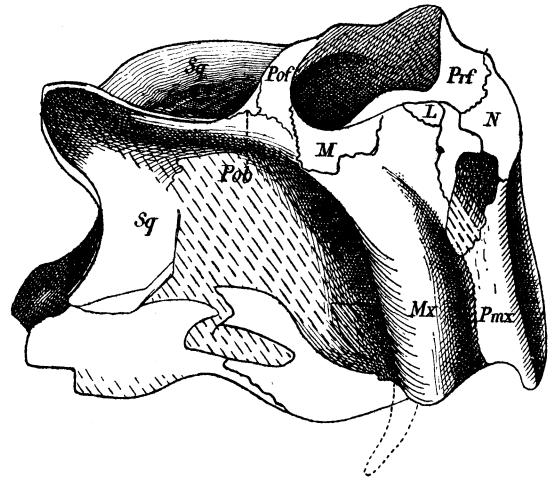


FIG. 2.

Fig. 1. *Lystrosaurus frontosus* Cope. An Anomodont from South Africa; skull from above. Fig. 2, do., from right side. The lower *Sq* is the supratemporal.

The South African genus *PROCOLOPHON* Ow. has been analyzed by Seeley* in an admirable manner. The orbit is greatly enlarged, so that the region of the bars is contracted. However, there is a zygomatic arch, an infratemporal foramen, and no supratemporal foramen, thus agreeing with the Theriodonts, and not with the Anomodonts.

In conclusion it appears that there are four types of crania represented in the Permian Reptilia, which are distinguished as follows:

Temporal roof uninterrupted	<i>Cotylosauria.</i>
A zygomatic arch, but no distinct supratemporal or supramastoid arches.....	<i>Theriodonta.</i>
Zygomatic and supratemporal arches	<i>Diopseus.</i>
No zygomatic; a supratemporal arch	<i>Anomodonts.</i>

* Philos. Trans. Roy. Soc., 1889, p. 269.

II. THE MESOZOIC REPTILIA.

We may now examine how far the cranial types above described continued into Mesozoic time, and ascertain whether any new forms appeared.

In the first place, *ÆTOSAURUS* Fraas presents a single foramen perforating an otherwise continuous roof of the temporal fossa. This foramen is bounded below by the postorbital and supratemporal bones. The postfrontal bone is closely joined to the parietal, and has no posterior extension except to the postorbital. The zygomatic arch is present and is continuous with the supratemporal and postorbital bones, there being no infratemporal foramen. These details are derived from Fraas' figures copied by Zittel in his *Handbuch der Paleontologie*.* In this figure no distinct zygomatic (quadratojugal), or supramastoid, is visible, but whether they are wanting or fused with adjacent elements, examination of specimens will best show. This genus is made the type of a suborder of Crocodilia by Baur (*Pseudosuchia*), but it appears to me to be typical of a special order (Pl. IV, Fig. 2).

The genus *ICHTHYOSAURUS* presents especial features. Here we have a zygomatic arch, and no infratemporal foramen. There is a superior foramen, however, which is bounded below by the postfrontal bone in front, and the supramastoid behind; which are themselves in contact below with the postorbital and the supratemporal. This foramen I call the supramastoid. A paroccipital bone is present in this genus, but no intercalare. See my memoir of 1870 above referred to (Pl. V, Fig. 1).

The *DINOSAURIA* may be represented by *Diclonius*, of which I have a complete skull before me (Pl. III). Here there are superior and inferior foramina which isolate two arches, of which the inferior is the zygomatic. The superior arch consists of the supramastoid bone posteriorly, and apparently the postfrontal anteriorly. The supratemporal, small in *Ichthyosaurus*, has now disappeared. There is a distinct paroccipital lying scale-like on the exoccipital. In *Diclonius* the supramastoid is fused with the parietal,† but in *Iguanodon*, according to Dollo, it is distinct.‡ The fact that the postfrontal and postorbital are not distinct from each other in the *Dinosauria* with which I am acquainted, makes the determination of the character of the superior arch somewhat difficult. This is probably the case in *Diclonius*, and is so represented by Dollo in *Iguanodon*. In a fine cranium of the Laramie *Laelaps incras-*

* Page 644, Fig. 569.

† Cope. *Proceeds. Acad. Phila.*, 1883, p. 110, Pl. V. In this description and plate the sutural lines supposed to separate the postfrontal from the postorbital and "squamosal" are of doubtful existence in the specimen.

‡ *Bulletin de Musée Royale d'Histoire Naturelle de Belgique*, II, 1883, p. 235, Pl. II.

satus Cope,* I find the bone in front of the arch to form two limbs of a nearly right-angled triangle, one of which is supraorbital, and the other postorbital. No suture divides it. It may represent the fused postfrontal and postorbital elements which we have in some Lacertilia. There is, however, a small free bone horizontally placed at the internal side at the posterior extremity of the supraorbital limb, which may be a postfrontal bone. In this case the anterior connection of the supramastoid bone will then be with the postorbital. This must however be clearly proven before it can be accepted, since it is the postfrontal bone † which articulates with the supramastoid posteriorly. If we suppose the long perpendicular postorbital process of the bone in question to represent the postorbital bone of *Ichthysaurus*, the question is simplified, but it is not certain that such is the case.

The figures given by Marsh of the "*Ceratosaurus*" *nasicornis* represent a structure similar to that of *Laelaps*, and similarly indecisive. The figures of *Hypsirhophus stenops*‡ (*Stegosaurus* Marsh) exhibit distinct postfrontal and postorbital bones. They show the postorbital produced upwards and backwards to form the horizontal bar with a posterior element. Between this element and the parietal is represented on one side of the figure another element, but this entire region is left undescribed in the text. The appearance given by one side of the figure (3) is that the supramastoid and supratemporal are both present, and that the latter is the posterior element in the bar. In that case the structure is that of the Theriodonta and Lacertilia, and not that of the Ichthyosauria.

The situation in the CROCODILIA appears to be the same as in the Dinosauria. Nothing satisfactory can be learned from the recent members of the order; and even in the skull of an *Alligator mississippiensis* one inch long, the postfrontal and postorbital bones are not distinct from each other. The Jurassic forms of the Teleosauridæ show the same character, and give the appearance of a postorbito-supratemporal arch.§ In the Triassic *Belodon* the structure seems to be essentially similar. The appearance in the PTEROSAURIA, as figured by authors, is the same as in the Dinosauria, but I cannot pronounce decisively in the lack of specimens. It is not unlikely that all the members of the Archosaurian series resemble each other in this respect, and I suspect that it is to be explained by reference to the Theriodonta. Here the postfrontal and postorbital are distinct, as already pointed out, but the former is small and is crowded by the adjacent elements. Its fusion with the post-

* Which I owe to the Geological Survey of Canada.

† Including the supposed squamosal of my description of *Diclonius* (*l.c.*).

‡ Amer. Jour. Sci. Arts., 1887, Pl. VI.

§ See Eudes Deslongchamps Notes Paleontologiques, 1863-9.

orbital would be probable. The arch is then supratemporal, and this element may be fused with the supramastoid in the Dinosauria.

If the RHYNCHOCEPHALIA of the Mesozoic had the same structure as Sphenodon, we may ascribe to them an infratemporal foramen and a zygomatic arch. The former is bounded above by a bar which consists anteriorly of the postorbital, and posteriorly, in all probability, of the supratemporal. Hence the postfrontal and supramastoid do not communicate as they do in the Ichthyopterygia; and the large foramen above the superior bar has different boundaries below from that observed in Ichthyosaurus, but is like that of the Anomodonts. Hence I call this foramen the

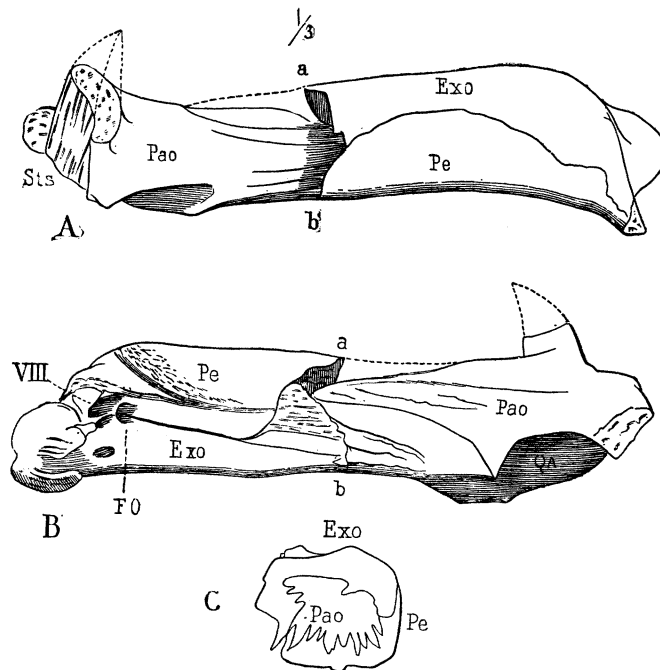


FIG. 3.

FIG. 3.—*Mosasaurus* sp., suspensorium of *os quadratum* of right side, one-third nat. size; from Greensand of New Jersey. *A*, from front; *B*, from behind; *C*, fractured end of proximal half seen at fracture, *a-b*; *Exo*, exoccipital; *Pe*, petrosal; *Pao*, paroccipital; *Sts*, suture for supratemporal; *QA*, articular surface for quadrate; *FO*, fenestra ovale; *VIII*, foramen for eighth nerve; *a b*, line of fracture.

supratemporal foramen, and the bar the supratemporal bar. In *Sphenodon* the paroccipital and supratemporal are fused together. The supramastoid is fused either with the supratemporal or the parietal (Fig. 9, Pl. II, and Fig. 3, Pl. IV).

In the PYTHONOMORPHA and LACERTILIA the zygomatic arch of the Rhynchocephalia has disappeared, leaving the superior or supratemporal arch only. That this is truly the supratemporal arch and not the supramastoid is shown by the fact that its anterior connection is with the postorbital as in *Sphenodon*, and not with the post-

frontal. I cannot agree with Baur that this arch in the lizards is the zygomatic arch of the other Reptilian orders. The supramastoid bone is, in the *Lacertilia*, wanting, but whether by atrophy or by fusion with the parietal, forming the supramastoid process of the latter, I do not know. An element intervenes between the supratemporal bone and the parietal above and the exoccipital within, which Dr. Baur regards as the supratemporal. With this I do not agree, and for the following considerations: In neither adult nor young *Lacertilia* is there present any other element which can be regarded as the homologue of the paroccipital of *Ichthyosaurus*, the *Testudinata* and *Dinosauria*. In the *Pythonomorpha* this element is deeply embraced between the petrosal (proötic) and exoccipital, precisely as is the paroccipital (Fig. 3). In the *Lacertilia* it is carried on the extremity of these elements. Moreover the supramastoid is a purely roof-bone, and has no connection primitively with the petrosal, and very little with the exoccipital. It cannot be identified with the supratemporal because it exists contemporaneously with that element in *Ichthyosaurus*,* as well as in the *Cotylosaurian* genera *Chilonyx* and *Pariotichus* above described. I therefore maintain the homology of this bone with the paroccipital as I presented it in my paper of 1870, where I used for it Huxley's term "opisthotic." (Pl. IV, Fig. 5). Parker, in his paper on the Development of the Skull in the *Lacertilia*,† did not discover a distinct ossification in the position of paroccipital, although he finds a portion of the exoccipital marked off by a shallow groove, which he calls opisthotic. The true paroccipital he calls the "second supratemporal."

In the *OPHIDIA* there is no zygomatic or supratemporal arch, and the supratemporal as well as the supramastoid bones have disappeared. The paroccipital is the only one of the suspensors of the quadrate remaining. This element had been generally homologized with the "squamosal" (supratemporal) by authors, but in my paper of 1870 I identified it with the paroccipital of the *Lacertilia* ("opisthotic;" supratemporal of Baur), with which Baur agrees. In the more specialized snakes its squamosal attachment to the cranial wall resembles that of the squamosal bones of higher *Vertebrata*, and its general position is that of that element. When, however, the lower snakes, *e.g.*, *Ilysia*, are examined, it is found to have the same position in the embrace of the exoccipital and petrosal bones, as in the *Pythonomorpha*, and to be clearly homologous with that element which I have thought to be the paroccipital (Pl. IV, Fig. 6).

In the *TESTUDINATA*, as pointed out by Baur, no foramina have been devel-

*The process of the parietal which joins the supramastoid arch in *Diclonius* (Plate III) may represent the supratemporal.

†Philosophical Transactions Royal Soc., 1879, p. 631.

oped, but the primitive roof has suffered diminution by absorption from the inferior edge, or from both the inferior and the posterior edges. In *Chrysemys*, where a bar has been produced (Pl. V, Fig. 5), it consists of the unseparated zygomatic and supratemporal, the anterior elements of which are the jugal and postorbital; and the posterior, the zygomatic and supratemporal. The supramastoid is wanting even in the genera (*Hydraspis e. g.*) with a parietoquadrate arch. The postfrontal and postorbital are not distinguished. In genera, where the posterior excavation is very deep (*e. g.*, *Trionyx*), the connection between the postorbital and the supratemporal is interrupted, and a zygomatic arch remains (Pl. V, Fig. 6). It was comparison of this type with the *Lacertilia* that led Baur* to conclude that the bar of the latter order is the zygomatic.

The SAUROPTERYGIA possess but a single arch, and this is the zygomatic according to the description of *Nothosaurus* given by Von Meyer. The supratemporal has no anterior connections according to this author, and the supramastoid is not described. From all that I can gather from Owen's descriptions and figures of *Plesiosaurus* the structure is the same; which is confirmed by observation on such imperfect specimens as are accessible to me. The postfrontal is not continued above the large temporal foramen; nor is the postorbital continued posteriorly. In the latter point the structure differs from that of the *Theriodonta*. The type of the *Sauropterygia* may be derived from that of the *Theriodonta* by the extension of the infratemporal foramen upwards to the parietal bone, thus cutting off the posterior connections of the postorbital and postfrontal bones. In this respect this type resembles the *Testudinata* (Pl. V, Fig. 4).

The Mesozoic reptiles (including the existing orders) present us then with the following types of postorbital structure:

I. One foramen; generally a zygomatic arch.

No supramastoid bone; postfrontal and postorbital fused; a paroccipital. *Testudinata*.
Postfrontal and postorbital distinct. *Sauropterygia*.

II. A supramastoid foramen only.

Supramastoid and zygomatic arches not distinguished from each other; a paroccipital,
Ichthyopterygia.

III. A supratemporal and infratemporal foramina.

Supramastoid and zygomatic arches. *Crocodylia*.
Dinosauria.
Pterosauria.
Rhynchocephalia.

* Amer. Journal of Morphology, 1889, p. 473.

IV. A supratemporal foramen only.

Zygomatic and supratemporal arches present and not separated by an infratemporal foramen,
Pseudosuchia.
 A supratemporal and no zygomatic arches; a paroccipital.....*Lacertilia.*
Pythonomorpha.

V. No arches or foramina.

Quadrate suspended to paroccipital.....*Ophidia.*

These structures must be considered in determining the systematic position of the groups above enumerated, but their characters are not all of equal systematic value.

III. THE PARIETOQUADRATE ARCH.

This arch is not present in the Batrachia, and is very variously developed in the Reptilia. It is produced by the separation of the posterior elements of the temporal roof of the Stegocephali and Cotylosauria, from the elements of the brain case below them. That is, by the development of a foramen between the supramastoid and supratemporal above, and the exoccipital and paroccipital below.

The parietoquadrate arch is a later appearance in geologic time. It is not present in any of the Permian orders. The earliest indication of it is seen in the Ichthyopterygia, where a space appears between the very large supramastoid above, and the exoccipital and paroccipital below. It is wanting in the three Archosaurian orders, but is represented by a fissure in the Triassic Belodon, and in Crocodilia in general.* In Testudinata it is potentially present in the posterior part of the temporal roof, but is only distinguished in certain Pleurodira (Hydraspis), where the supramastoid element is lost, or fused with the parietal processes which form its proximal part. In the Rhynchocephalia it is well developed in Sphenodon, but here also the supramastoid element is not distinct, being fused with either the supratemporal or parietal. The arch has the same character in Lacertilia, except that the paroccipital sends upwards a brace along its inferior border. That this element is the paroccipital has been already shown by reference to the structure in the Ichthyosaurus and in the Pythonomorpha (Fig. 3).

The space enclosed below the parietoquadrate arch I propose to call the parietoquadrate foramen. Its presence is an indication of systematic value, but not in general of a high grade. Thus among the Squamata it is absolutely wanting in Ophidia, and is scarcely elevated above the exoccipital in some Pythonomorpha. In Lacertilia the foramen is much reduced in Feylinia, and is wanting in Anniella and the Amphisbænia, while it is large in most other types.

* See Deslongchamps, E., Notes Paleontologiques, I, 1868-9, Caen et Paris.

IV. SYSTEMATIC CONSIDERATIONS.

From the preceding facts certain results follow. The knowledge of the Permian types enables us to trace the affinities of the orders of later ages with much more precision than has been possible hitherto. In the first place, we derive the Testudinata directly from the Cotylosauria, which realizes the theoretical type which Baur correctly supposed to have given origin to all the later orders. Thus we need not look for the ancestry of the Testudinata in any other group. This order then constitutes Series I.

As Series II we can take up the line in which the supramastoid foramen appears (Ichthyopterygia). This type is not clearly marked out in the Permian, but according to Baur the Triassic *Mixosaurus* presents an approximately terrestrial form of Ichthyosauria, which can be probably traced to Permian ancestors. This series does not seem to have been continued, but this is not to be assumed, as yet, without further evidence.

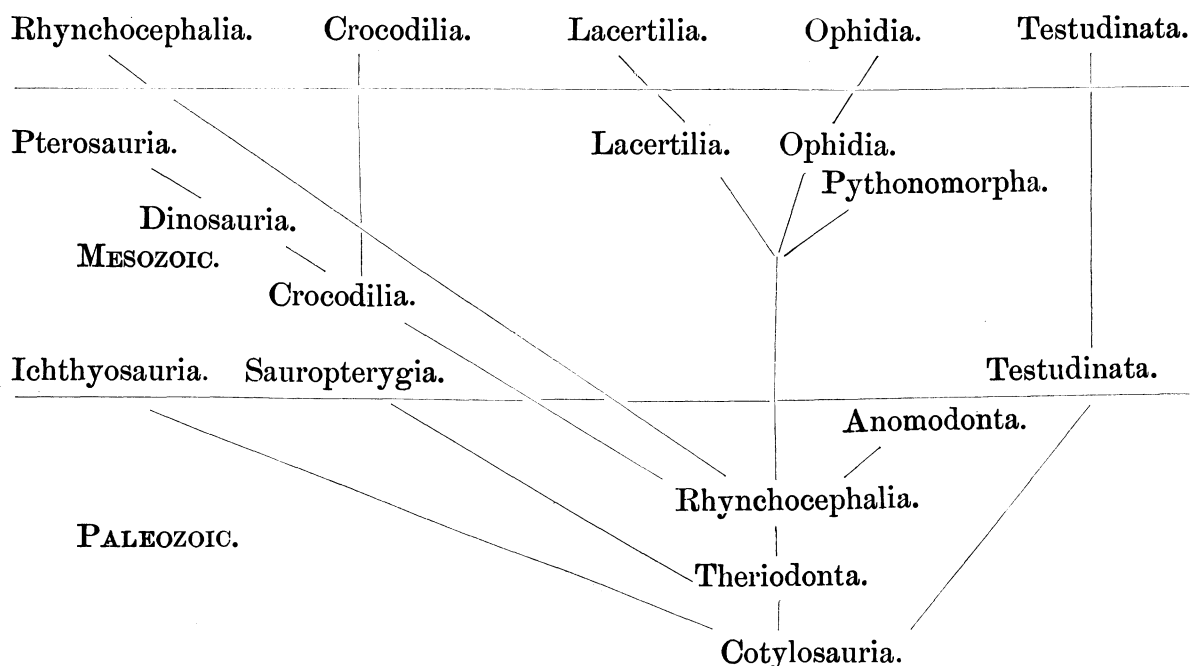
As Series III we commence with the Permian Theriodonta, where an infratemporal foramen is first developed. In *Diopseus* a supratemporal foramen appears. The latter represents the type of the Rhynchocephalia, and probably the Dinosauria, Crocodilia and Pterosauria. The loss of the supratemporal bar and preservation of the zygomatic gives us the Sauropterygia. The loss of the zygomatic arch only, gives us the Anomodontia; and the non-sutural articulation of the quadrate gives us the Squamata. The loss of both the supratemporal and zygomatic bars gives us such Lacertilia as *Heloderma* and *Anniella*, and the Ophidia.

The importance of the connections of the posterior bars of the skull is for the first time appreciated in the present paper. It is difficult to learn these connections from the writings of authors, so completely have they been neglected. For instance, the terms postfrontal and postorbital are sometimes used indifferently by Marsh in describing the crania of Dinosauria. It is true that in a few Lacertilia, as the Varani, these elements are fused together. The supramastoid and supratemporal elements have been generally confused except in the Ichthyosauria, where both exist together. It may be alleged that the difference between the supramastoid and supratemporal bars is not great, and that the one might have been readily transformed into the other. But this supposition will not bear examination. When the one bar has been established the other has been lost, and a recovery after such loss is not probable. This follows from the fact that the position of a bar is the result of the loss of the Cotylosaurian roof from all other regions. The only case where the reduction has not at first restricted the roof to the position of one bar or the other, is that of

the Testudinata, where both sets of elements are included in a single bar. This compound bar is, however, reduced to the zygomatic elements in the more specialized forms, and is not unfrequently entirely lost.

Aided by these considerations we get the following phylogenetic series. Each one of them originated in the Permian epoch. This table resembles essentially the one I gave in the article on the Evolution of the Vertebrata in the American Naturalist for 1885, p. 247, in which all the later orders were traced to the Theromora, the Lacertilian series through the Rhynchocephalia. The varied character of that assemblage was not at that time suspected, but it is true that there is a great resemblance between the orders now included in it, except in the matter of the cranial roof and bars, and in the nature of the rib-articulations. The discovery that Diopseus is allied to the Rhynchocephalia places that order in immediate relation with the Theromorous series on the one hand; while a correct estimate of its cranial structure places it in immediate relation with the Lacertilia on the other.

RECENT.



The five reptilian series might be then further defined as follows:

- Quadrate fixed; no supramastoid or supratemporal foramen or separate arch. *Theromora*.
- Quadrate fixed; a supramastoid foramen and arch. *Ichthyopterygia*.
- Quadrate fixed; a supratemporal and zygomatic arch. *Archosauria*.
- Quadrate fixed; a zygomatic arch only. *Synaptosauria*.
- Quadrate free; no supramastoid foramen or arch; a supratemporal but no zygomatic arch. *Streptostylica*.

The Theromora are the earliest in time, and their order of Theriodonta presents the nearest affinities to the Mammalia. The Cotylosauria, on the other hand, display the nearest relations to the Stegocephalous Batrachia.

In the following illustrations the phylogenetic successions are indicated by diagrams based on the skull of *Pantylus cordatus*. This is adopted as the most convenient of the Cotylosaurian types to be taken as a standard, because it displays none of the especial peculiarities that characterize *Chilonyx*, and is better known in the lateral posterior region than *Pariotichus*. In the series which terminates in the *Streptostylica* we commence with the Theriodont type in Fig. 1, with an infratemporal foramen only, and reach *Diopseus* or *Sphenodon* with both infratemporal and supratemporal. This is naturally followed by *Dicynodon* with supratemporal foramen and no zygomatic arch, from which we pass to the Lacertilia, which has the free os quadratum. The descent of the Lacertilia is from the Theriodonta through the Rhynchocephalia, the Anomodontia being a lateral branch. The Archosaurian line may commence with a form with a supramastoid foramen only, or one with an inframastoid only. We know no type of the latter kind; and of the former we have the aquatic Ichthyopterygia. A terrestrial type of this order probably existed, which represents the stock from which the Archosaurian line is derived. In this series the order of development probably has been Crocodilia, Dinosauria, Pterosauria, as represented in Figs. 9 and 10, Pl. V.

EXPLANATION OF PLATES.

Plate I.

STEGOCEPHALI AND COTYLOSAURIA.

Fig. 1. *Mastodonsaurus giganteus* Jaeger, $\frac{1}{2}$ nat. size; from Fraas.

2. *Chilonyx rapidens* Cope, $\frac{3}{8}$ nat. size; from above; premaxillary, maxillary, jugal and zygomatic regions restored; *a*, left side. Coll. E. D. Cope.
3. *Pariotichus megalops* Cope, $\frac{3}{8}$ nat. size; zygomatic region imperfect; from above; *a*, left side. Coll. E. D. Cope.
4. *Pantylus cordatus* Cope, $\frac{3}{4}$ nat. size; occipital region imperfect; from above; *a*, right side. The line passing through the postorbital, postfrontal and supratemporal is a fracture of the osseous roof. Coll. E. D. Cope.

Plate II.

THERIODONTA AND RHYNCHOCEPHALIA.

Fig. 5. *Edaphosaurus pogonias* Cope, $\frac{3}{8}$ nat. size; with imperfect zygomatic region, seen obliquely from above; *a*, posterior view. Coll. E. D. Cope.

6. *Clepsydrops natalis* Cope, $\frac{3}{4}$ nat. size; with superior posterior part of skull imperfect; left side. Coll. E. D. Cope.

- Fig. 7. Naosaurus claviger* Cope, $\frac{1}{4}$ nat. size ; muzzle and lower jaw wanting, but restored from allied species ; zygomatic arch partly wanting ; left side ; *a*, from above. Coll. E. D. Cope.
8. *Diopelus leptocephalus* Cope, $\frac{1}{2}$ nat. size ; supratemporal, zygomatic and quadrate bones ; left side. Coll. E. D. Cope.
9. *Sphenodon punctatum* Gray, skull $\frac{3}{4}$ nat. size ; right side. Coll. E. D. Cope, from Sir James Hector, New Zealand.

Plate III.

DICLONIUS MIRABILIS Leidy ; skull about one-fourth natural size, from side and above.

Plate IV.

DIAGRAMS OF SKULLS OF THE THEROMORO-STREPTOSTYLICATE SERIES ; vertical and side views, based on *Pantylus cordatus*.

- Fig. 1. Theriodonta. Fig. 2. Pseudosuchia* (from Zittel). *Fig. 3. Rhynchocephalia. Fig. 4. Anomodontia. Fig. 5. Lacertilia. Fig. 6. Ophidia.*

The supramastoid-parietal suture is omitted in the Pseudosuchia to resemble Aëtosaurus. The supratemporo-supramastoid suture is omitted in the Rhynchocephalia in imitation of Sphenodon. All the teeth but one are omitted from the Anomodontia, in imitation of Dicynodon.

Plate V.

THE ARCHOSAURIAN AND SYNAPTOSAURIAN SERIES ; DIAGRAMS OF SKULLS, based on *Pantylus cordatus*.

- Fig. 1. Ichthyosauria. Fig. 2. Crocodilia* (Teleosaurus). *Fig. 3. Dinosauria* (Diclonius). *Fig. 5. Sauropterygia* (Nothosaurus). *Fig. 6. Testudinata* (Chrysemys). *Fig. 6. Testudinata* (Trionyx).

In the Crocodilia and Dinosauria the supratemporal is omitted, and in Sauropterygia it is fused with the supramastoid. In Testudinata the supramastoid is omitted. In Dinosauria the postorbital and postfrontal are represented as fused, although this may be an appearance only.

EXPLANATION OF LETTERING.

Pmx., premaxillary bone ; *Mx.*, maxillary ; *J.*, jugal (malar) ; *Z.*, zygomatic (quadratojugal) ; *L.*, lachrymal ; *N.*, nasal ; *F.*, frontal ; *Pef.*, prefrontal ; *Pof.*, postfrontal ; *Pob.*, postorbital ; *P.*, parietal ; *Sm.*, supramastoid ; *St.*, supratemporal ; *Int.*, intercalare ; *So.*, supraoccipital ; *Bo.*, basioccipital ; *Q.*, quadrate ; *Pg.*, pterygoid ; *Stap.*, Stapes.

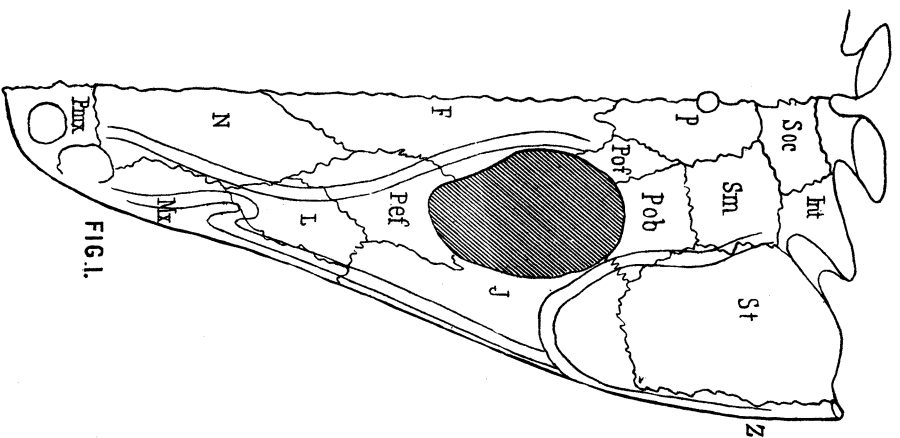


FIG. 1.

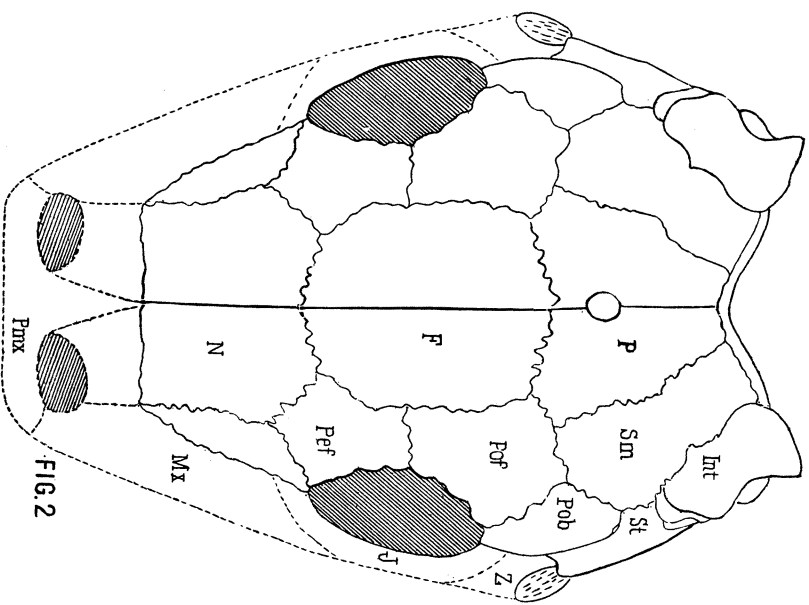


FIG. 2.

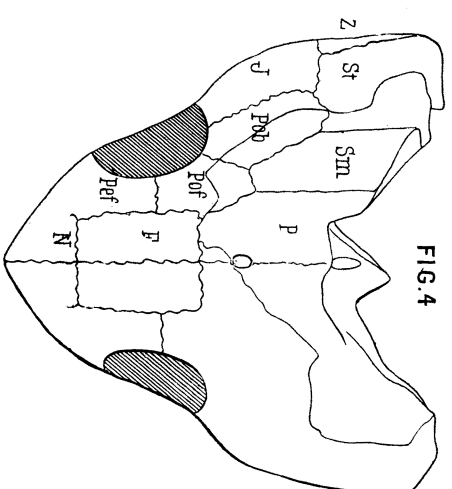


FIG. 4.

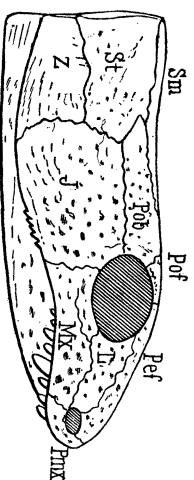


FIG. 4A.

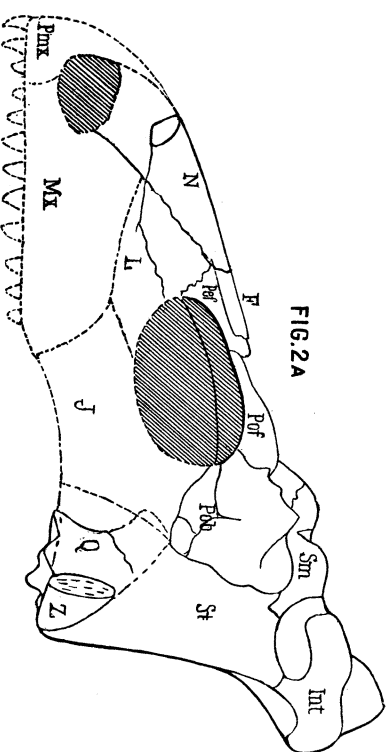


FIG. 2A.

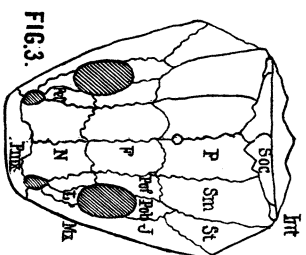


FIG. 3.

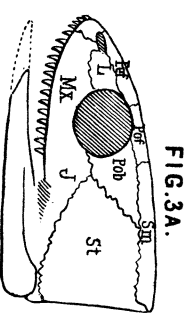
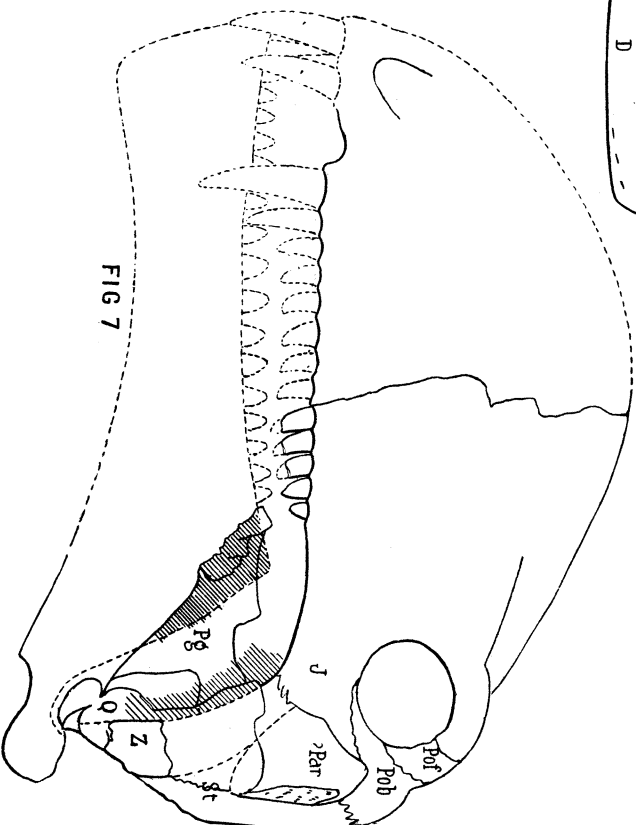
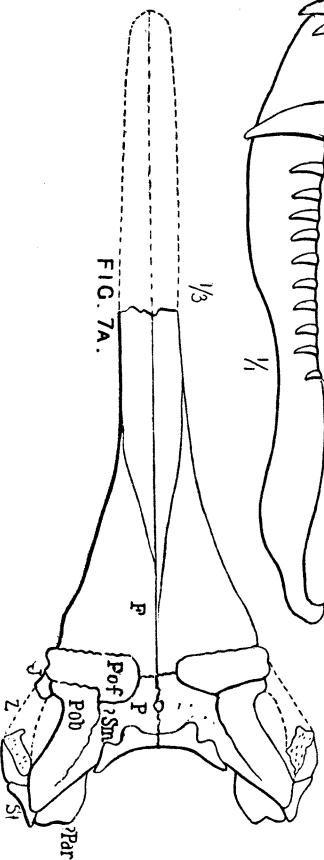
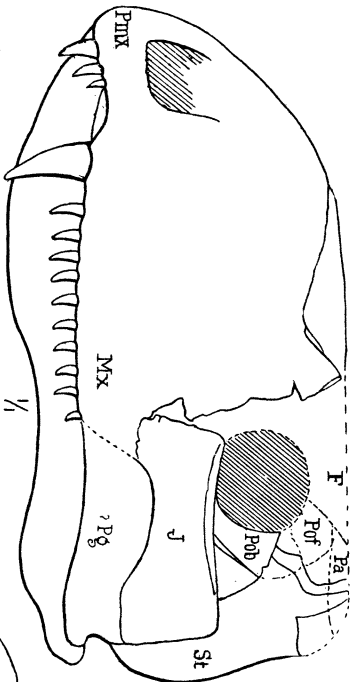
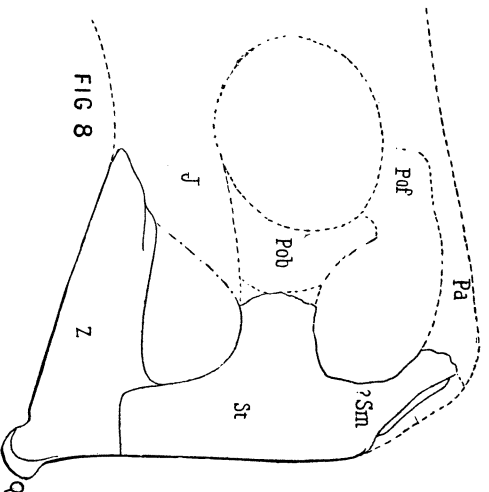
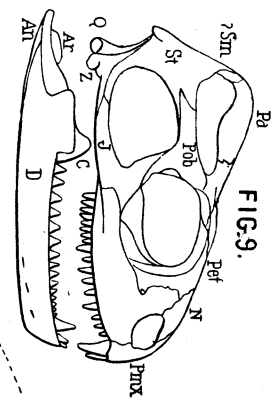
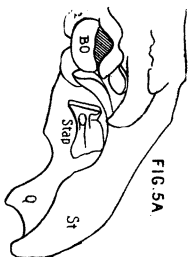
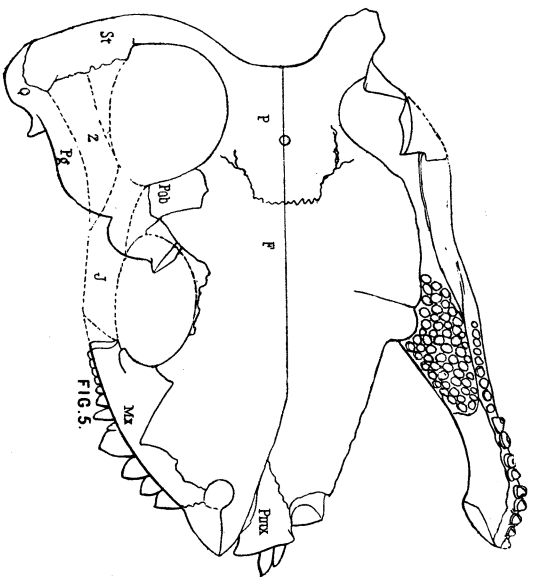
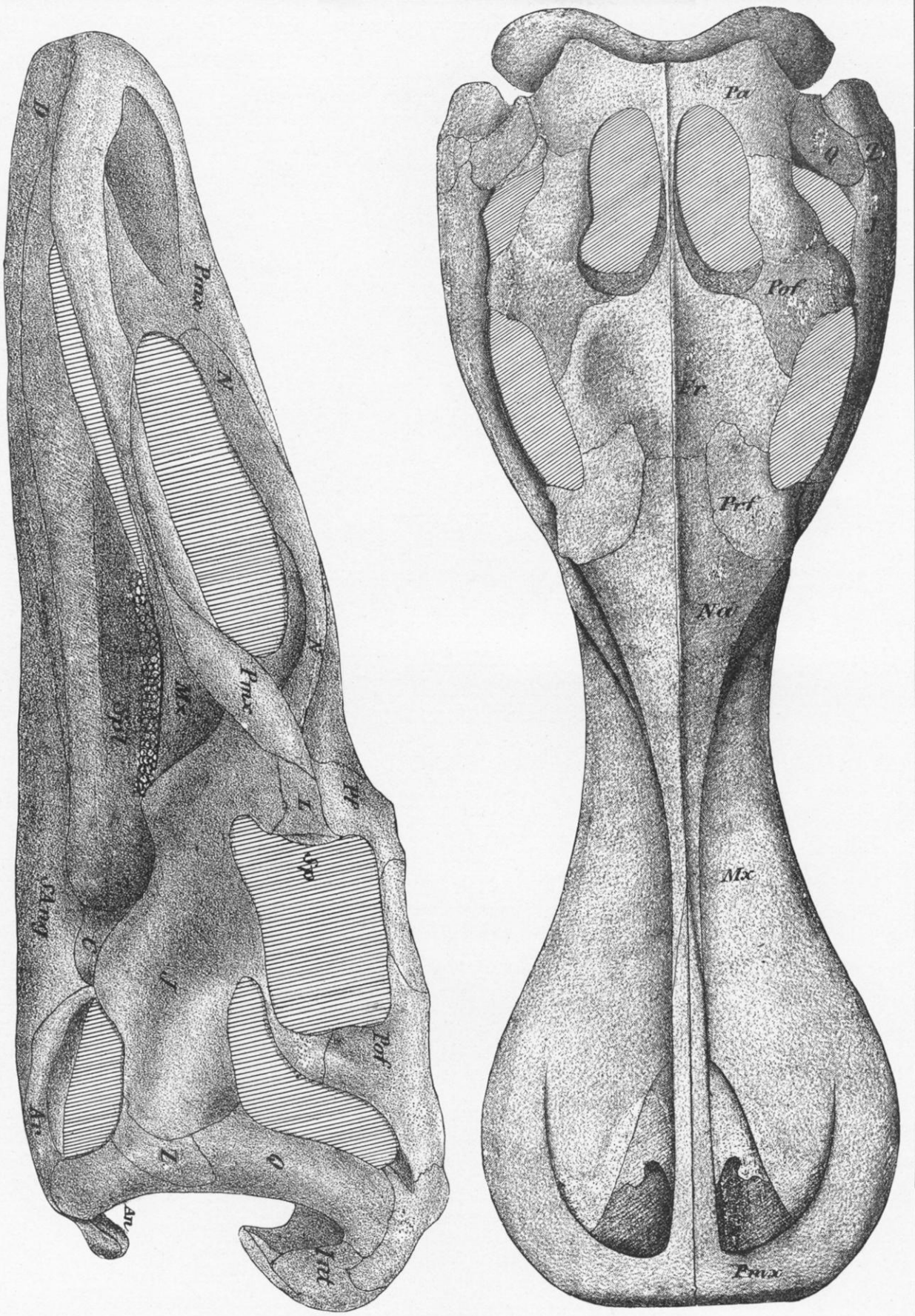


FIG. 3A.





Diclonius mirabilis.

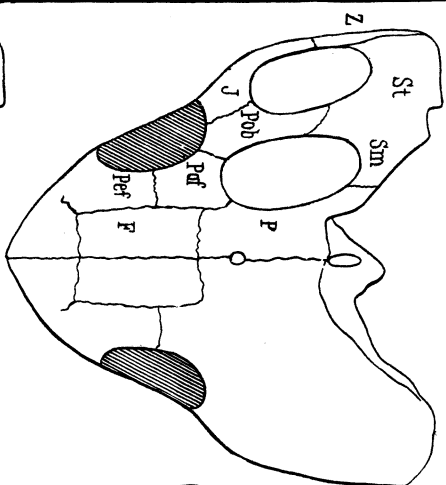


FIG. 3.

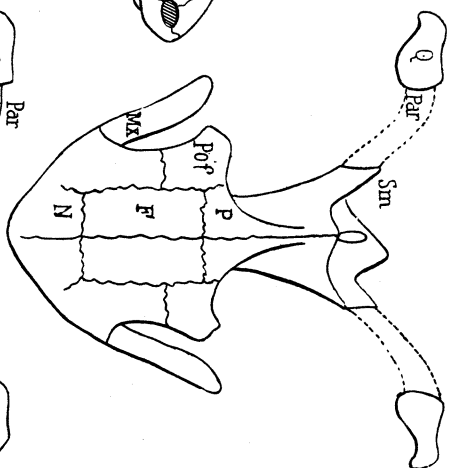
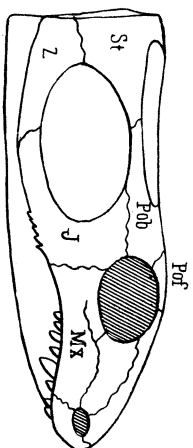


FIG. 6.

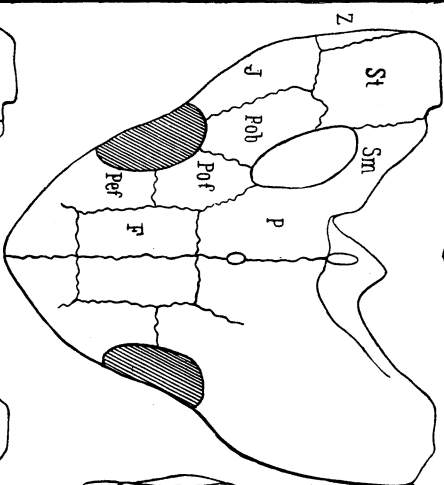
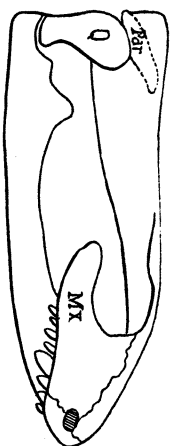


FIG. 2.

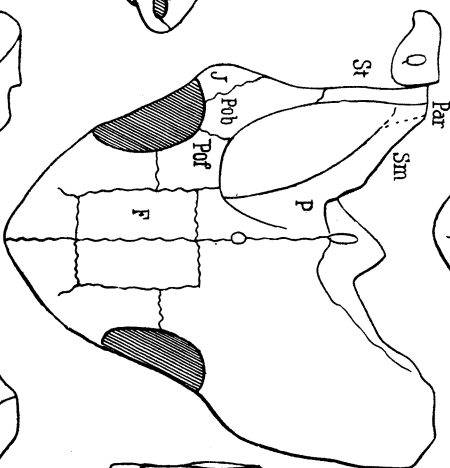
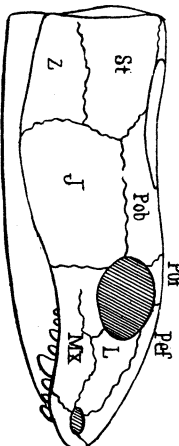


FIG. 5.

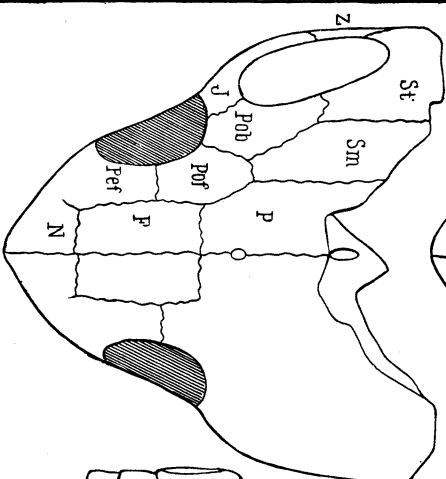
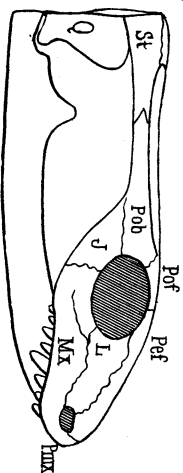


FIG. 1.

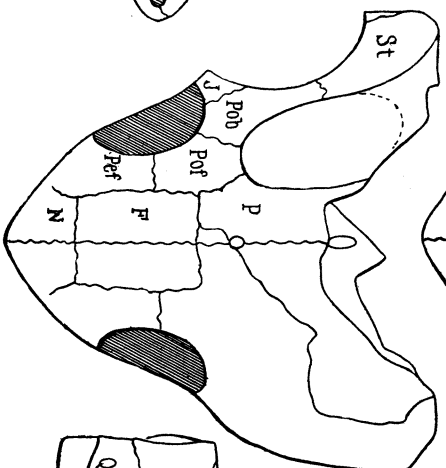
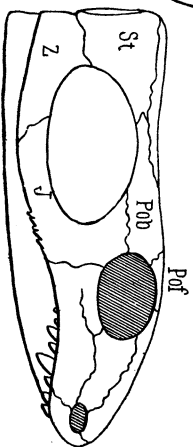
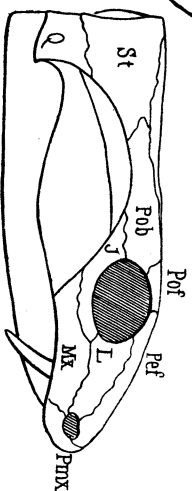
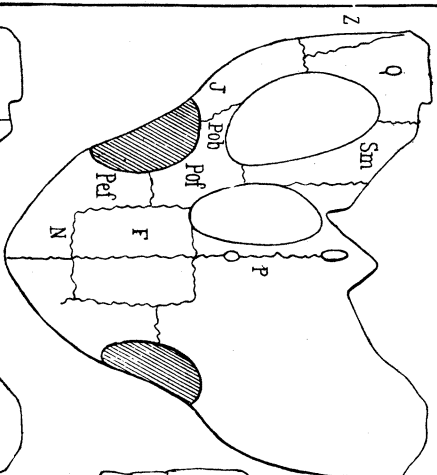


FIG. 4.





. FIG. 3

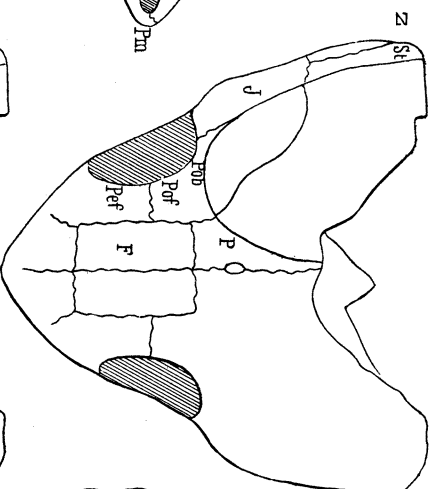
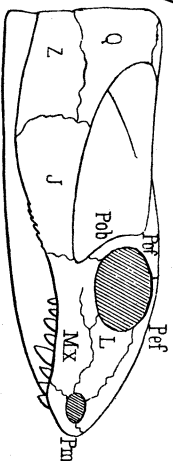


FIG. 6.

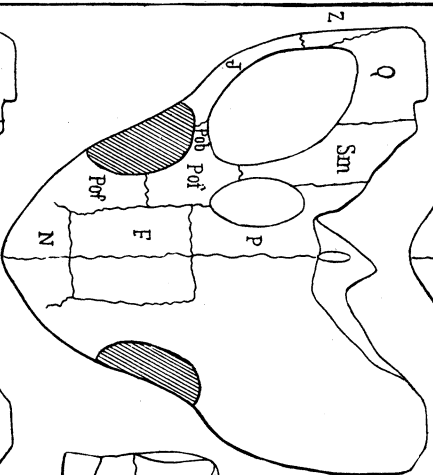
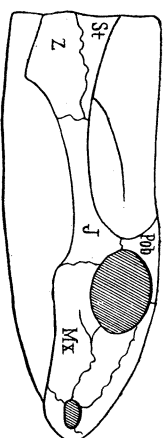


FIG. 2.

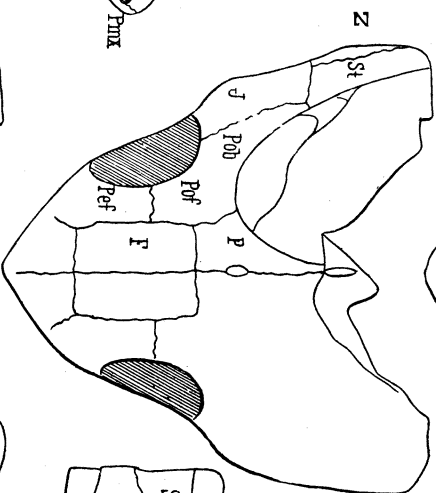
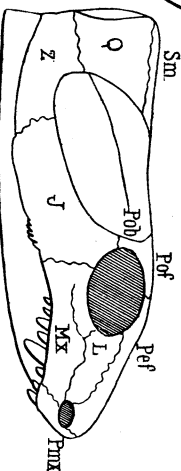


FIG 5

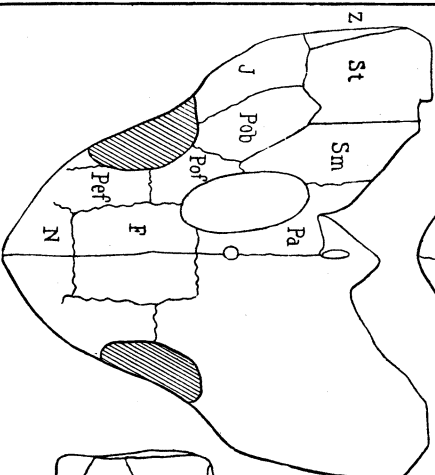
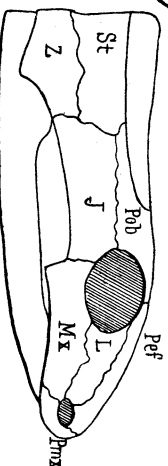


FIG. 1

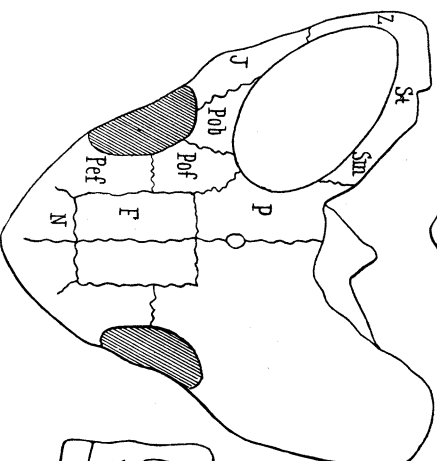
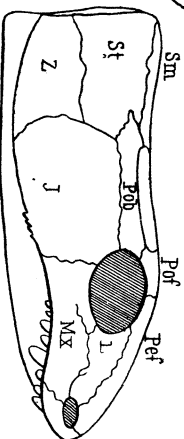


FIG. 4.

